A TETRAPOD TRACKWAY FROM THE CARBONIFEROUS OF NORTHERN CHILE

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ABSTRACT. A tetrapod trackway, comprising ten footprints, is described from the Carboniferous rocks of the Chinches Formation, northern Chile. The trackway was apparently made by an amphibian. It is the first fossil referable to a tetrapod to be reported from the Carboniferous of any of the present-day continental areas which once made up the Palaeozoic continent of Gondwanaland. Its discovery strengthens the argument that the southward drift and consequent cooling climate of Carboniferous Gondwanaland need not necessarily have resulted in the complete extinction of the indigenous tetrapod stocks (known from the Devonian rocks of the continent) but may simply have restricted their distribution.

WE report below the occurrence of a series of footprints made by a tetrapod vertebrate in Carboniferous rocks of the Chinches Formation, in the Andes of northern Chile. The location (26° 58′ S., 68° 55′ W.) is in Quebrada Colorado, 8 km east of Salar de Maricunga and to the north of the road between Copiapo and Tinogasta (text-fig. 1).

Tetrapod fossils of Carboniferous age have previously been described only from Europe and North America, and have not hitherto been recorded from any of the present-day continental areas which once comprised the Palaeozoic continent of Gondwanaland. The trackway from Chile is thus of considerable palaeobiogeographical importance and clearly merits description, despite the fact that circumstances have so far prevented either the specimen or a cast of it from being collected.

STRATIGRAPHIC AND PALAEOENVIRONMENTAL SETTING

The Palaeozoic sedimentary rocks between 26° and 28° S. in northern Chile occur in two geographically distinct areas. Those in the coastal region (Las Tortolas Formation) are deep-sea basin-plain turbidites (Bell 1982), which were deformed in an accretionary wedge produced by north-east directed subduction, possibly during Carboniferous times (Bell 1984). These sediments are separated from those in the east (Chinches Formation) by a graben containing Mesozoic and Cenozoic sedimentary, volcanic, and plutonic rocks. The strata of the Chinches Formation, which in Quebrada Colorado comprise siltstones with minor proportions of mudstone and very fine-grained arkosic arenite, are much less deformed than those in the coastal region and have been subjected to only very low-grade metamorphism. Correlation between the isolated exposures (see text-fig. 1B) is based on stratigraphic and lithologic comparisons. The strata containing the footprints, in Quebrada Colorado east of Salar de Maricunga, are lithologically, sedimentologically, stratigraphically, and structurally similar to the more extensive exposures to the south-west of Salar de Maricunga (including Quebrada Chinches). There is therefore little doubt that they form part of the same succession.

The Chinches Formation in Quebrada Colorado and elsewhere is unconformably overlain by rhyodacites and ignimbrites of the Pantanoso Formation and intruded by granitoids. In some places the Pantanoso Formation overlies the granitoids; in others it is intruded by them. The Pantanoso Formation (equivalent to the Choiyoi Formation of western Argentina) is usually designated as Permian to Triassic in age (Mercado 1982; Coira *et al.* 1982), although Sepulveda and Naranjo (1982) suggested an earlier, Carboniferous, age for at least part of the succession. Their suggestion was based on the unconformably overlying Las Represas Formation, which contains ammonites of

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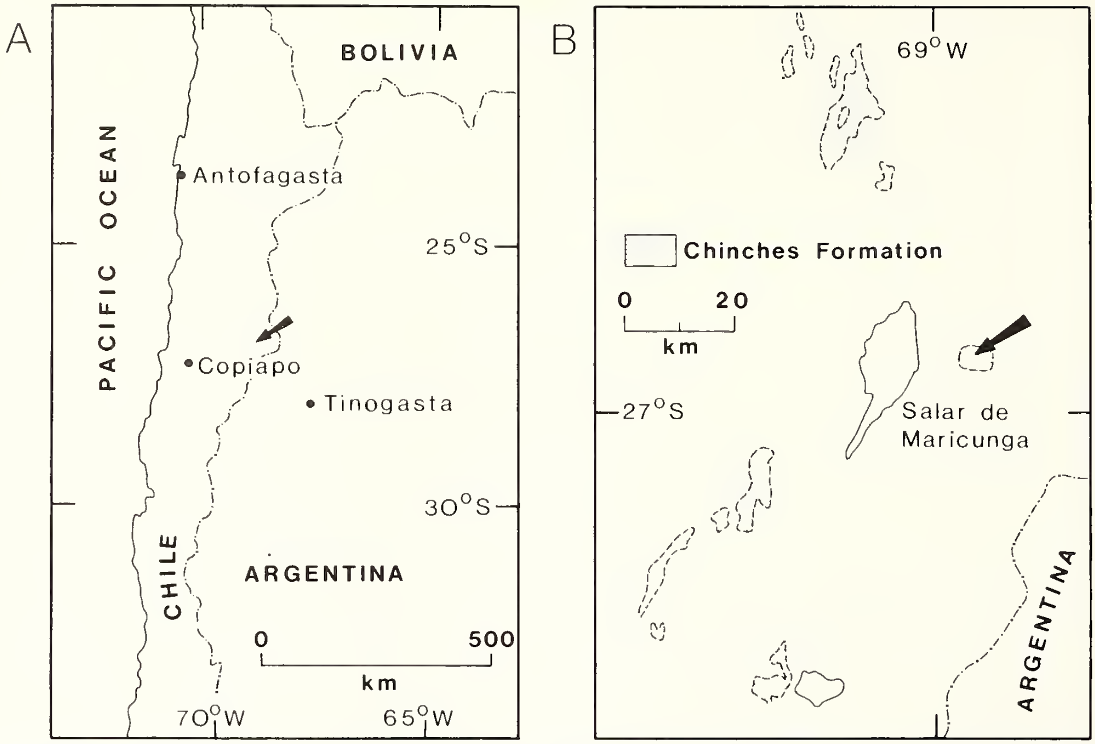


TEXT-FIG. 1. Location of trackway. A, map of northern Chile and adjacent countries. Arrow indicates trackway locality; B, map of area around Salar de Maricunga. Exposures of Chinches Formation stippled. Arrow indicates trackway locality.

Lower Permian age. The only absolute ages available for the granitoids intruded into the Chinches Formation are 287±4 Ma and 260±5 Ma (K–Ar biotite), suggesting an Upper Carboniferous to Lower Permian age for the granitoids themselves and supporting the suggestion of a Carboniferous age for the Chinches Formation. Palaeoniscoid fish scales from the Quebrada Chinches are regarded by Professor D. L. Dineley (Department of Geology, University of Bristol) as being probably early Carboniferous in age (pers. comm. to senior author). However, in view of the K–Ar dates, noted above, for the granitoids intruded into the Chinches Formation, and of the paucity of the biostratigraphic evidence, we do not think it justifiable at this stage to date the strata containing the tetrapod trackway any more precisely than as Carboniferous.

Possible depositional environments for the Chinches Formation include tidal flats (suggested by Sepulveda and Naranjo (1982) mainly on the basis of the presence of stromatolites), lagoonal or lacustrine. Modern mud-dominated tidal flat and lagoonal deposits do exhibit facies similar to those in the Chinches Formation but differ significantly in the presence of channels and bioturbation, and of interstratified alluvial or aeolian deposits in the tidal sequences (Fisk 1959; Thompson 1975; Elliott 1978). A lacustrine origin is favoured for the Chinches Formation, based on:

1. The presence of only a sparse fauna and flora (the former including bivalve molluscs but no purely marine invertebrate taxa) in a shallow-water environment which was probably well-oxygenated (the sand grains have rims of iron oxide and the rare plant remains are preserved only as impressions).

2. The presence of sedimentary structures and lithologies characteristic of lacustrine depositional facies (see Galloway and Hobday 1983; Link and Osborne 1978; Picard and High 1972; Sturm and

Matter 1978). These include parallel laminated deep-water facies, shallow wave-dominated facies and lake shore facies.

3. The presence of thin stromatolitic and pisolithic horizons in a predominantly fine-grained pelitic sequence (see Picard and High 1972; Sanders 1968; Schafer and Stapf 1978; Surdam and Wolfbauer 1975).

DESCRIPTION

The terminology employed for the trackway measurements in the following description is that proposed by Peabody (1948).

The trackway, as preserved, measures 1·1 m in length and comprises ten positive imprints (two are poorly preserved but the remaining eight are shown in text-fig. 2) on a smooth and gently undulating bedding plane of very fine-grained sandstone. The five clearest consecutive footprints are shown in text-fig. 3 and also, with measurements, in text-fig. 4. The width of the trackway at this point is 18·8 cm. The stride is 29·5 cm and the pace angulation 101°. Two differing measurements of pace (17·9 and 20·2 cm) may be made on the basis of the pes imprints present in this, the only section of the trackway sufficiently well preserved for proper analysis, giving a mean value of 19·05 cm. The manus, which like the pes is turned forward so that its mid-line is roughly parallel to that of the trackway itself, appears to bear five digits. The digits are of moderate length and show no obvious signs of webbing. None of the pes imprints certainly shows the presence of more than four digits, but it is probable that five were actually present in the animal responsible for the trackway.

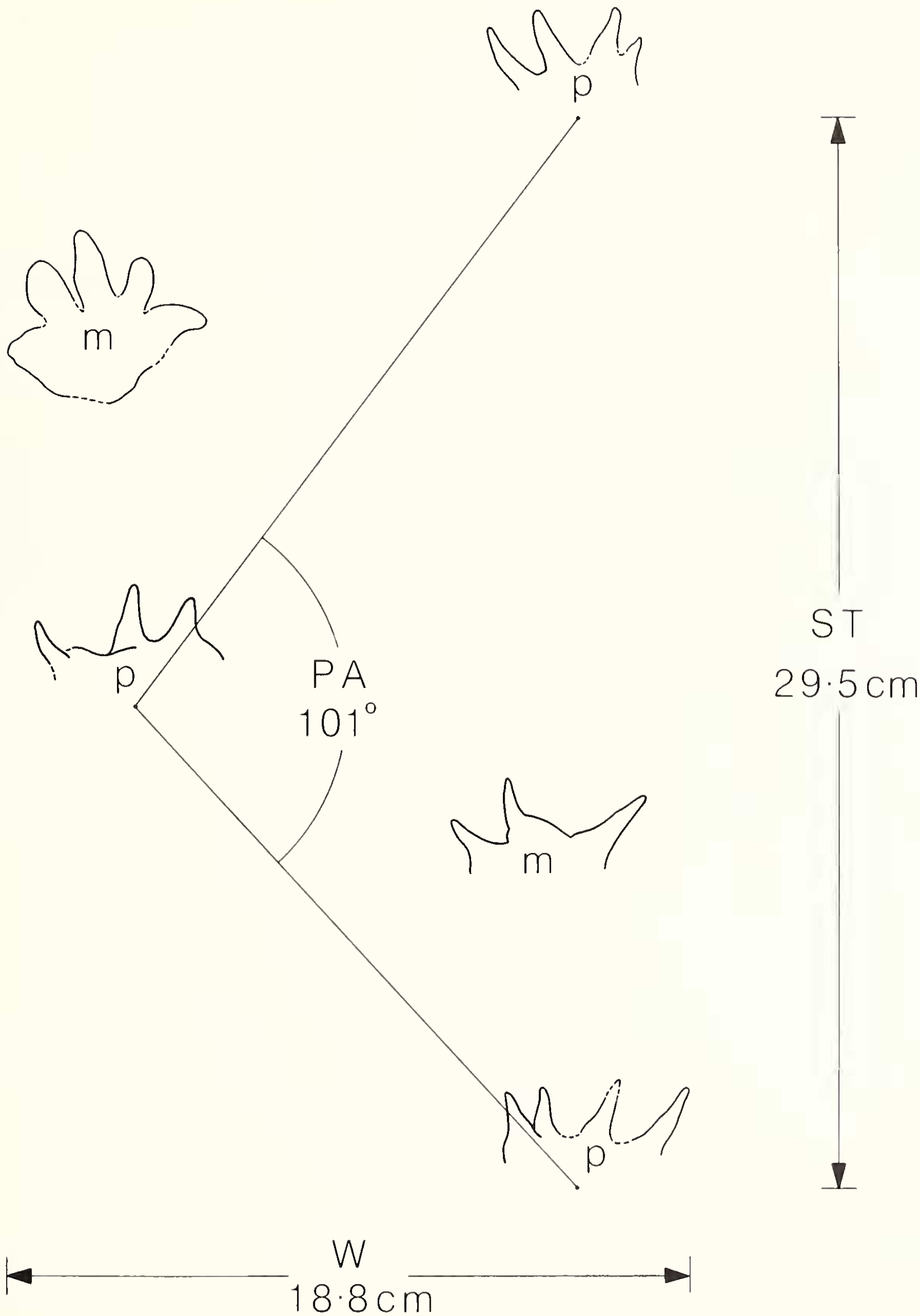
TEXT-FIG. 2. Section of trackway, showing eight footprints (×0·25). Tape measure graduated in centimetres.

Although some Palaeozoic tetrapods (such as the temnospondyl and microsaur amphibians) possessed fewer than five digits in the manus, five was the number commonly present in the pes. The appearance of most of the pes imprints in the trackway, in which the visible impressions of the digits are more or less widely separated from one another at their proximal ends, suggests the presence of partial webbing which depressed the substrate so that only the free part of each digit normally left a clear trace. The trackway exhibits no evidence of a tail drag.

TEXT-FIG. 3. Detail of trackway, showing five footprints (×0·55 approx.). Tape measure graduated in centimetres.

Using the method outlined by Baird (1952, pp. 833–834) for determining the approximate distance between the pectoral and pelvic girdles of a trackway-making amphibian or reptile, a body length (excluding head and tail) of about 26 cm may be estimated for the animal which made the trackway that forms the subject of the present study. However, as pointed out by Baird, the method makes no allowance for the curvature of the vertebral column during locomotion, so the distance calculated is likely to be slightly less than the actual gleno-acetabular distance.

That the trackway was made by an amphibian rather than by a reptile is suggested by the absence of claw and epidermal scale impressions and (although less strongly) by the apparent presence of webbing between the digits of the pes. However, more detailed consideration of the relationships of the tetrapod responsible for the Quebrada Colorado trackway (and a more detailed description of the trackway itself) must await collection of the specimen.



TEXT-FIG. 4. Detail of trackway, showing measurements. Dotted lines indicate restored areas. Abbreviations: W—width; ST—stride; PA—pace angulation; m—manus; p—pes.

DISCUSSION

As noted above, the trackway from Quebrada Colorado represents the first recorded evidence of Carboniferous tetrapods from anywhere outside Europe and North America. During the Devonian and Carboniferous the latter two regions together formed a large part of the continent of Laurasia, which also included Greenland and Russia west of the Ural Mountains. South America, however, was a constituent of the great southern continent of Gondwanaland, as also were Africa, Antarctica, Australia, and India (e.g. Tarling 1980; Johnson 1980). Although no tetrapod fossils have hitherto been described from the Carboniferous of any of the present-day geographical areas which once made up Gondwanaland, amphibians of Devonian age have been reported from Brazil and south-east Australia (Gondwanaland) as well as from East Greenland (Laurasia). The Brazilian material consists of only a single footprint, described by Leonardi (1983) as *Notopus petri*. It is, however, very well preserved and is apparently of late Givetian or early Frasnian age; *Notopus* may thus be the earliest known tetrapod. The described Australian specimens comprise three trackways from the Frasnian of Victoria (Warren and Wakefield 1972) and an isolated lower jaw (*Metaxygnathus*) from the late Frasnian or early Famennian of New South Wales (Campbell and Bell 1977). The ichthyostegalian amphibians from the late Famennian of East Greenland are, however, represented by relatively abundant material, and three genera (*Ichthyostega*, *Ichthyostegopsis*, and *Acanthostega*) have been described (Säve-Söderbergh 1932; Jarvik 1952). Ichthyostegalian affinities have been suggested for the Australian Devonian amphibians and also, although with less certainty, for that from Brazil.

The evidence at present available is not adequate to determine with any sureness whether the area of origin of tetrapods lay in Devonian Gondwanaland or in Devonian Laurasia (no tetrapod fossils at all have been described from the Devonian or Carboniferous of Angaraland, the third major Upper Palaeozoic continent (Johnson 1981)). However, the fact that *Notopus* may be of late Givetian (Middle Devonian) age and hence significantly older than *Metaxygnathus* and the footprints from Victoria, which are in turn older than the Greenland ichthyostegalians, does lend support to the suggestion made by Panchen (1977) and Janvier (1978) that the first tetrapods arose in Gondwanaland. Migration of terrestrial and freshwater tetrapods from Gondwanaland to Laurasia may well have been possible in the Upper Devonian. As Johnson (1980, 1981) has pointed out, similarities in the Upper Devonian structural history, stratigraphy and freshwater fish faunas of south-east Australia and East Greenland suggest that these two areas were in close proximity at this time.

During the Carboniferous, Laurasia appears to have continued the northward drift it had exhibited during the Devonian but nonetheless remained largely within the tropics, the tetrapods apparently migrating southward to remain within the tropical belt (Johnson 1981; Panchen 1973, 1977). In contrast, Gondwanaland drifted southward and by early Upper Carboniferous times this drift, and the accompanying rotation of the continent, had brought south-east Australia close enough to the South Pole for the area to suffer sea-level glaciation (Johnson 1981). Johnson (1981) has suggested that the southward drift and cooling climate of Carboniferous Gondwanaland must have compelled the indigenous tetrapods to migrate northward and eventually resulted in their extinction on that continent. This view received support from the absence (until now) of any records of post-Devonian tetrapods from Gondwanaland prior to its early Permian collision with Laurasia, which event allowed colonization from the latter continent.

The trackway described in the present paper is obviously of considerable interest as the first reported non-Laurasian Carboniferous tetrapod specimen, and as the latest known specimen which can be regarded with some confidence as representing the original, indigenous, tetrapod fauna of Gondwanaland. However, it inevitably also raises the question of whether the indigenous tetrapods of the latter continent did indeed all become extinct between the Upper Devonian and the end of the Carboniferous, as argued by Johnson. Carroll and Gaskill (1978, p. 196) have suggested that the Carboniferous cooling of Gondwanaland may merely have restricted the distribution of the indigenous tetrapods, and that the lack (at the time they wrote) of records of Carboniferous tetrapods from the modern areas which once made up the continent probably had more to do with geological and modern cultural patterns than with the ecology and biogeography of Carboniferous times. This argument is clearly strengthened by the discovery of the Quebrada Colorado trackway; the question, however, can finally be resolved only by further field-work in the dispersed fragments of Gondwanaland.

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